# Niche-based processes explaining the distributions of closely related subterranean spiders

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## Abstract

**Aim:** To disentangle the role of evolutionary history, competition and environmental filtering in driving the niche evolution of four closely related subterranean spiders, with the overarching goal of obtaining a mechanistic description of the factors that determine species' realized distribution in simplified ecological settings.
**Location:** Dinaric karst, Balkans, Europe.
**Taxon:** Dysderidae spiders (*Stalita taenaria*, *S. pretneri*, *S. hadzii* and *Parastalita stygia*).
**Methods:** We resolved phylogenetic relationships among species and modelled each species' distribution using a set of climatic and habitat variables. We explored the climatic niche differentiation among species with *n*-dimensional hypervolumes and shifts in their trophic niche using morphological traits related to feeding specialization.
**Results:** Climate was the primary abiotic factor explaining our species' distributions, while karstic and soil features were less important. Generally, there was a high niche overlap among species, reflecting their phylogenetic relatedness, but on a finer scale, niche shifts explained the realized distribution patterns. Trophic interaction was another important factor influencing species distributions – the non-overlapping distributions of three morphologically indistinguishable *Stalita* species is seemingly the outcome of competitive exclusion dynamics. The distribution of the fourth species, *Parastalita stygia*, overlaps with that of the other species, with several instances of coexistence within caves. As inferred from the morphology of the mouthparts, the mechanism that minimizes interspecific competition is the shift in the trophic niche of *P. stygia* towards a more specialized diet.
**Main conclusions:** We showed that similarity in niches only partly correlated with the phylogenetic distance among species, and that overlaps in species distributions are possible only when a parallel shift in diet occurs. Our work emphasized how even simplified environments still maintain the potential for diversification *via* niche differentiation. Ultimately, we provide an ecological explanation for the diversification of life in an important hotspot of subterranean diversity.

**Keywords:** cave-dwelling spider, Dysderidae, ecological niche, MaxEnt, n-dimensional hypervolume, niche shift, phylogeny, species distribution modelling, subterranean biology, troglobiont

# 1 | INTRODUCTION

The idea that species can thrive within a specific set of environmental conditions, loosely their ecological niche, is central to ecology and evolution. The study of species' niches provides a conceptual foundation for understanding historical and current distribution patterns, ultimately allowing us to predict with some confidence how species will respond to climate change and other environmental modifications (Chase & Leibold, 2003). One of the most popular representations of the niche is the *n*-dimensional hypervolume (Hutchinson, 1957), whereby the geometry of the niche space is approximated as an abstract Euclidean space defined by *n* independent axes that correspond to abiotic and biotic factors affecting the organismal performance (Blonder, 2018a; Blonder et al., 2014; Holt, 2009). The recent proliferation of a variety of statistical methods to estimate these multidimensional spaces (e.g. Mammola & Cardoso, 2020) have fuelled a renewed interest in exploring theoretical aspects related to the niche theory, such as the study of the eco-evolutionary process that shapes the geometry of a niche in space and time (Blonder, 2018a; Holt, 2009), but also more applied topics (e.g. Hanson et al., 2020). In spite of these advances, it remains notoriously challenging to tease apart the potential role of abiotic constraints and interspecific interactions in driving morphological and ecological niche shifts.

To approach niche-based studies, ecologists have typically used species within a given clade to explore if their niches are evolving, and if so, how fast and for what reasons (Holt, 2009; Liu et al., 2020). Typical models in this sense are radiations of surface-dwelling species (Gillespie et al., 2020), such as Darwin finches (Grant & Grant, 2008), *Anolis* lizards (Gavrilets & Losos, 2009) and cichlid fish (McGee et al., 2020). Yet, in most surface settings, the wide variability of the abiotic conditions and the great diversity of organisms and interactions represent important confounding factors that may limit our ability to disentangle niche-based processes. In contrast, the subterranean ecosystem is simpler, providing an ideal setting for eco-evolutionary studies (Mammola, 2019a; Mammola, et al., 2020; Sánchez-Fernández et al., 2018). Subterranean habitats are among the most widespread terrestrial ecosystems on Earth (Culver & Pipan, 2019; Ficetola et al., 2019; Mammola, et al., 2019) which, unlike most surface systems, may persist relatively unchanged for millions of years (Gibert & Deharveng, 2002). The absence of light and scarcity of nutrients limit the diversity and abundance of resident species, and the largely constant climatic conditions often translate into a narrow ecological niche for species that have adapted to life in caves (Culver & Pipan, 2019). A similar simplified setting should permit to characterize the abiotic and biotic axes that define the niche of subterranean species with more confidence, and to approximate species interactions simply as the overlap in the resulting niche geometries.

We chose a group of closely related spiders in the family Dysderidae, which occur in caves across the northern part of the Dinaric karst, to explore mechanisms underlying niche evolution. Previous work on niche evolution among specific lineages of spiders has concluded that niche shifts, potentially resulting from interspecific competition, can permit co-occurrence in some areas (Kennedy et al., 2019), while in other areas, niche shifts were associated with abiotic variables, without co-occurrence (De Busschere et al., 2010). Among cave species, the role of abiotic constraints in shaping the geometry of the niche has often been emphasized (Mammola & Isaia, 2017a). Conversely, biotic interactions have long been considered of secondary importance in the evolution of cave life (e.g. Poulson & White, 1969), until different authors recently reassessed the role of competition as a potentially important selective force in subterranean species (e.g. Culver & Pipan, 2015; Fišer et al., 2012; Mammola, 2019a; Trontelj et al., 2012). Recent studies discussed how interspecific interactions may be involved in driving morphological differentiation in coexisting cave spiders (e.g. in *Dysdera* in the Canary island; Arnedo et al., 2007 and *Troglohyphantes* in the Alps; Mammola, et al., 2018; Mammola, et al., 2020). Other studies suggested the potential role for interspecific interactions in determining segregation of species along environmental gradients in caves (e.g. Mammola et al., 2016; Resende & Bichuette, 2016), as well as shift in diet, activity patterns (e.g. Novak et al., 2010) and climatic preferences (Mammola & Isaia, 2017b).

Here, we set out to examine the interplay between these processes by first mapping current distribution ranges of our model species and exploring their phylogenetic relationships. We then reconstructed the shape of their ecological niche using *n*-dimensional hypervolumes (Blonder et al., 2014), and disentangled the ecological processes underlying niche differentiation (Mammola & Cardoso, 2020). We finally interpreted niche overlaps in the light of shifts in dietary requirements, as inferred using morphological traits. We tested the following predictions:

**1**. the closer two species are from a phylogenetic standpoint, the more similar their niche space should

be – a phenomenon termed 'niche conservatism' (Peterson, 1999; Wiens & Graham, 2005);

**2**. insofar as competition requires spatial proximity, the higher degree of niche overlap should be attained in species with disjunct distributions;

**3**. species whose distributions overlap should show divergent morphologies (e.g. cheliceral and fang morphology; Arnedo et al., 2007; Rezač et al., 2008) that could serve to minimize direct competition and facilitate coexistence.

By linking niche differentiation to morphological and phylogenetic similarities among species, our overarching goal was to obtain a mechanistic description of the factors that determine each species' realized distribution.

# 2 | MATERIALS AND METHODS

## 2.1 | Model species and study area

Dysderidae Koch, 1837 (Arachnida: Araneae), is a Western Palearctic family of spiders, whose representatives are frequently found in caves around the Mediterranean basin (Mammola et al., 2018). They do not build webs, but instead actively hunt their prey. Here, we focused on four species belonging to genera *Stalita* Schiödte, 1847 (Figure 1a) and *Parastalita* Absolon & Kratochvíl, 1932 (Figure 1b), both belonging to the Rhodinae subfamily. These species are restricted to the northern half of the Dinarides and are highly specialized for subterranean life (Kratochvíl, 1970). Genus *Stalita* has four nominal species: *S. taenaria* Schiödte, 1847, *S. hadzii* Kratochvíl, 1934, *S. pretneri* Deeleman-Reinhold, 1971, and *S. inermifemur* Roewer, 1931. Considering the limited number of records (two caves only), we excluded *S. inermifemur* from the analysis. *Parastalita* is a monotypic genus with one species, *P. stygia* (Joseph, 1882), found to co-occur in several caves with *S. taenaria* and *S. pretneri*. *Parastalita* is easily differentiated from *Stalita* species by its elongated and horizontal chelicerae (which, in *Stalita*, are perpendicular to the ground), while morphologically, the three *Stalita* species are virtually identical and can be differentiated only by inspecting copulatory organs (Deeleman-Reinhold, 1971; Kratochvíl, 1970).

The Dinarides (Dinaric Alps) is a mountain range in the western Balkans, whose carbonate part, the Dinaric karst, harbours more than 20,000 caves (Zupan Hajna, 2019) and is a global hotspot of subterranean biodiversity with more than 900 obligate subterranean species (Culver et al., 2006; Sket, 2012; Sket et al., 2004). With 101 species, spiders are the second-most numerous terrestrial group in Dinaric caves after beetles (Pavlek & Ribera, 2017; Platania et al., 2020; Sket et al., 2004; Wang & Li, 2010).

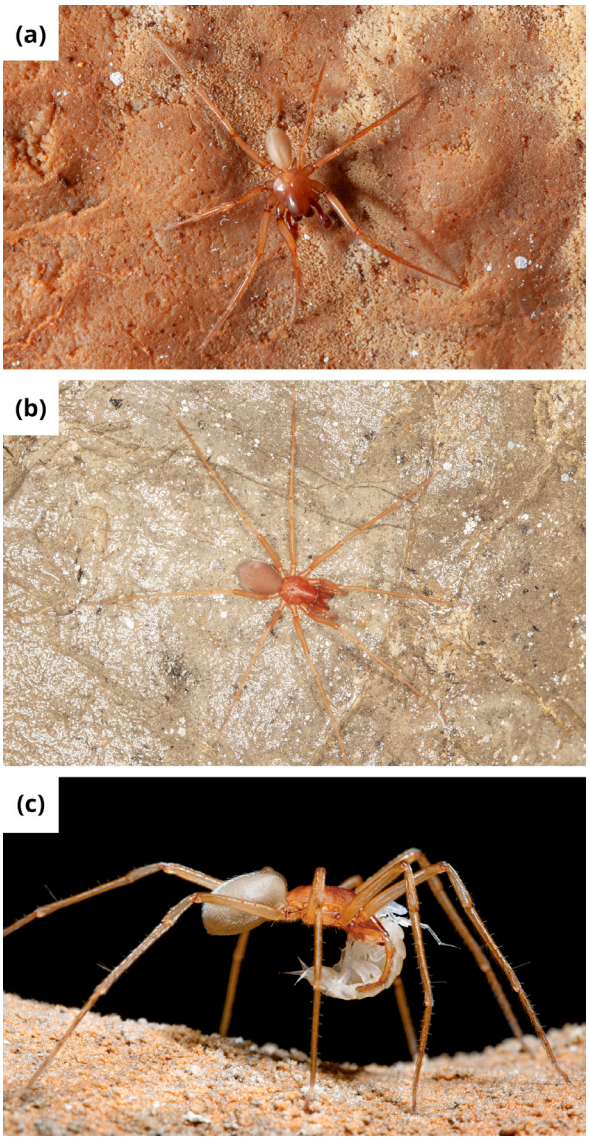


**Figure 1 | (a)** *Stalita taenaria* Schiödte, 1847; photo credit Helena Bilandžija, **(b)** *Parastalita stygia* (Joseph, 1882); photo credit Jana Bedek, **(c)** *P. stygia* feeding on a woodlouse *Alpioniscus iapodicus* Bedek, Horvatović & Karaman, 2017; photo credit Kazimir Miculinić

## 2.2 | Molecular procedures and phylogenetic analyses

In order to explore phylogenetic relationships among the four studied spiders, we selected representatives of each of them, as well as of the other three Rhodine

genera so as to capture the whole subfamily diversity. For *Mesostalita*, we included two of three known species, for *Rhode* two of eight, and for *Stalitella* we included the only known species. Furthermore, we selected a representative for each of the other two Dysderidae subfamilies, Harpacteinae and Dysderinae. The list of the samples used and their GenBank® accession codes are available in Appendix S1.

The laboratory procedures of genomic DNA extraction and PCR amplifications follow Platania et al. (2020). We amplified fragments of five genes: the mitochondrial genes encoding cytochrome *c* oxidase subunit I (COI) and ribosomal RNA 16S, and the nuclear genes for histone H3 and ribosomal RNA 28S and 18S. The information on the primers used, amplification protocol as well as the profiles for the PCR amplifications are available in Appendix S1. We sent unpurified PCR products to the Macrogen services for sequencing. We assembled, reviewed and edited sequence chromatograms of each sample with Geneious v. 8.1.9 (Kearse et al., 2012). We automatically aligned all genes using default options in the Geneious plugin of the alignment program MAFFT v. 7.017 (Katoh et al., 2002), and concatenated them in a super matrix with 19 terminals: 676 bp of the COI, 976 bp of the 16S, 810 bp of the 18S, 853 bp of the 28S and 328 bp of the H3. We inferred the best maximum likelihood tree with IQ-TREE v. 2.0 (Minh et al., 2019). First, we used ModelFinder to select the best-fit partitioning scheme and corresponding evolutionary models (Kalyaanamoorthy et al., 2017), and then we inferred the best tree topology and estimated clade support by means of 1,000 replicates of non-parametric bootstrapping. We used MrBayes v3.2.6 (Ronquist & Huelsenbeck, 2003) to implement Bayesian inference. We assessed the best partitioning scheme and corresponding evolutionary model with Partition Finder v2.1.1 (Lanfear et al., 2017). The analysis was run for 30 million generations, sampling each 1,000, with eight simultaneous Markov Chain Monte Carlo chains, 'heating temperature' of 0.15 and an initial burn-in of 10%. We expressed support values as posterior probabilities. We monitored the convergence of the chains, the number of burn-in generations and correct mixing with Tracer v. 1.7 (Rambaut et al., 2018).

### 2.3 | Species distribution modelling

We conducted all ecological analyses in R (R Core Team, 2018). We used species distribution modelling (SDM) to map the distribution of our model species in the Dinaric karst and to identify key environmental predictors driving the observed distribution patterns. Although we acknowledge that SDM is a correlative way to estimate species range, having large uncertainties and often over- or underfitting the real distribution, it still proved useful for answering a wide range of ecological questions (>6,000 studies up to now; Araújo et al., 2019).

#### 2.3.1 | Occurrence data

We assembled a dataset with georeferenced records for the four species (Figure 2) based on material deposited in the collection of the Croatian Biospeleological Society, the collections of the Universities of Ljubljana and Barcelona, the private collection of Roman Ozimec and on an extensive survey of literature (see https://doi.org/10.6084/m9.figshare.12613193). Occurrences datasets for cave-dwelling species are often unevenly distributed in space due to the fact that most speleological research is concentrated in more easily accessible caves and karst areas (Mammola & Leroy, 2018). To avoid local overexpression of the numbers of occurrences as a result of sampling heterogeneity, we performed a spatial correction of occurrence points of each species. We tested different spatial corrections: (a) a sampling bias grid at the resolution of the environmental predictors, or (b) a sampling bias grid and subsequent spatial thinning of occurrence points based on minimum distances of 0.01, 0.02 and 0.05 relative to the species range, as implemented in the 'red' package (Cardoso, 2017). Given that models fitted with occurrences corrected using the first approach performed better for all species (as measured with Boyce index; see later), we kept this spatial correction protocol in all analyses.

#### 2.3.2 | Environmental predictors

To depict subterranean conditions across north Dinarides, we selected a combination of topographical, bioclimatic, geological and soil variables (Table 1), all at a resolution of 30 arc-sec. A shape file of the hydrogeological map of Dinaric karts was obtained from the Diktas project website (http://diktas.iwlea rn.org/), providing layers that represent aquifers with different levels of permeability. Specifically, two Karst-fissure layers, one with good and the other with moderate permeability, two Intergranular layers with good and moderate permeability (we combined those into categorical variable 'Intergranular'), and lastly, one layer with poor permeability and another with impermeable rocks which we combined into the category 'Impermeable'. We rasterized all these shapefiles and used them as categorical binary predictors. We downloaded bioclimatic variables and elevation data from the

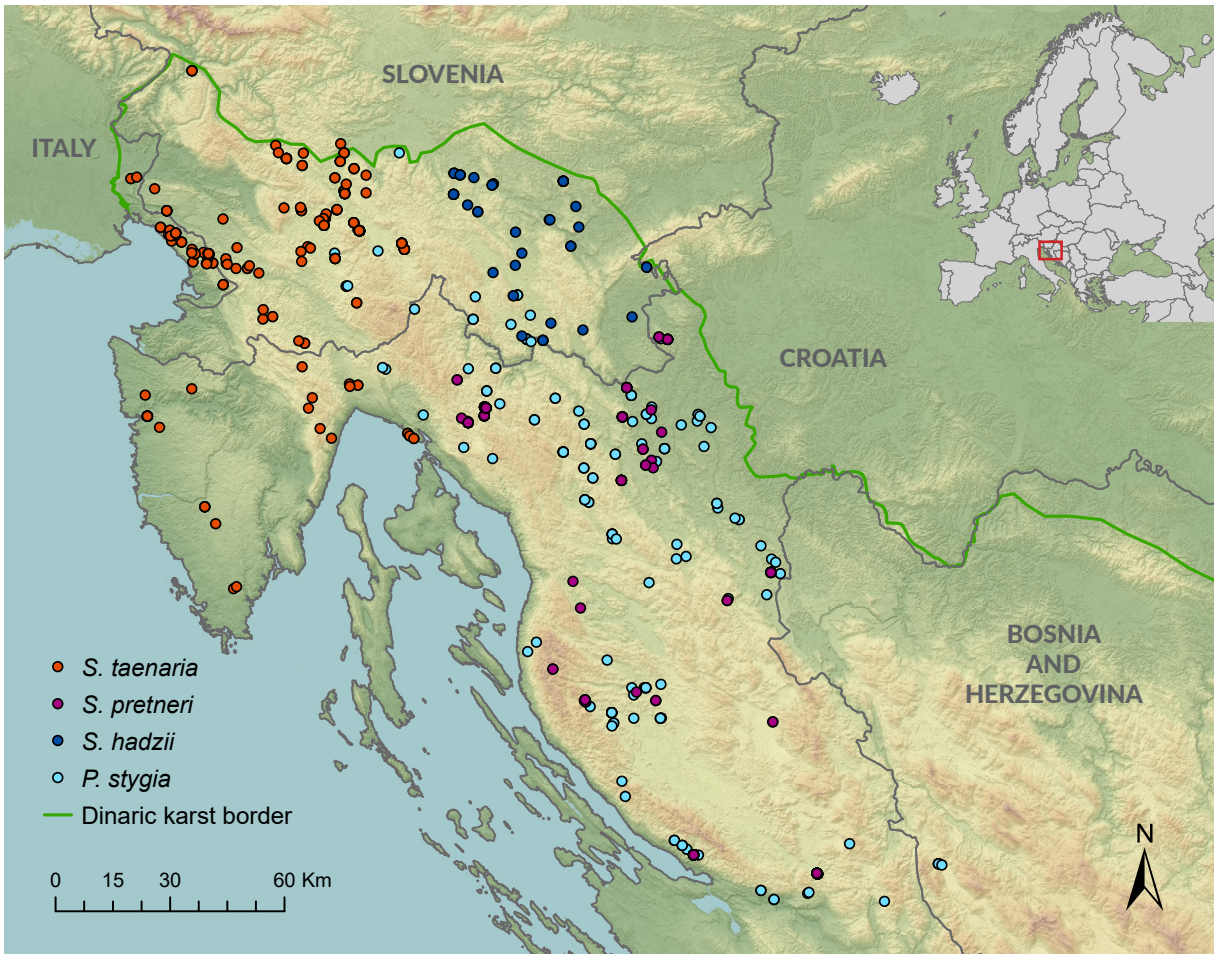


**Figure 2** | A map with occurrence records of *Stalita taenaria, S. pretneri, S. hadzii* and *Parastalita stygia*

WorldClim website (Fick & Hijmans, 2017), and extracted rasters of soil properties from SoilGrids database (Hengl et al., 2017).

We tested multicollinearity (Braunisch et al., 2013) among continuous predictors using Pearson *r* correlation, setting a threshold for culling collinear variables at $|r| > 0.7$. We inspected relationships between continuous and categorical variables graphically using boxplots (Zuur et al., 2010).

### 2.3.3 | Accessible area

We calibrated each SDM within the accessible area, namely, the geographic extent that a certain species was supposedly capable of occupying throughout its evolutionary history (Barve et al., 2011). Because we had no quantitative knowledge on the actual dispersal potential of our model species within the Dinaric karst, we used half the distance between the two distant-most occurrences of each species to approximate it. We buffered each species occurrences by a radius equivalent to this distance, and combined all circles in a final shapefile that we used to crop the environmental predictors. We also faced an issue related to data limitation because the shape file of the hydrogeological map does not extend beyond Dinaric karst in the north-western part. That is why we were forced to artificially cut the accessible area at 46.2 North and 21.0 West. However, we believe this is a reasonable assumption given that our model species are not found on non-soluble rock, meaning that areas outside the Dinaric karst should be unsuitable for species dispersal anyway.

### 2.3.4 | Modelling procedure

As we lacked reliable absence data for our model species, we constructed SDMs using a presence-only algorithm (MaxEnt), with the function *maxent* in the 'dismo' R package (Hijmans et al., 2014). Considering that we had <100 independent records for most of the species,

**Table 1 |** Variables selected in the species distribution models and their relevance to represent subterranean conditions (rationale for inclusion). Non-collinear variables introduced in the model are highlighted in bold

| Variable name | Acronym | Source | Rationale for inclusion |
|---|---|---|---|
| **Average temperature [°C]** | **Temp** | Fick & Hijmans, 2017 | In general, average annual temperature outside corresponds to the internal temperature of caves (Badino, 2010) |
| **Precipitation [mm]** | **Prec** | Fick & Hijmans, 2017 | Precipitation regime influences general underground climatic conditions (Badino, 2010). It is also a proxy for the overall input or organic matters (Culver et al., 2006). |
| Precipitation average [mm] | Prec_avg | Calculated from Prec | |
| Water vapor pressure [kPa] | Vap | Fick & Hijmans, 2017 | A proxy for subterranean moisture content. |
| Solar radiation [kJ m-2 day-1] | Srad | Fick & Hijmans, 2017 | Influences microclimate of superficial subterranean habitats (Mammola et al., 2016) |
| Elevation [m] | Dem | Fick & Hijmans, 2017 | Elevation has a general influence on climatic conditions (Badino, 2010). |
| Distance from the LGM ice [km] | Ice | Mammola, Schönhofer, & Isaia, 2019 | Reflects the impact of Pleistocene glaciations on subterranean fauna (Mammola, Schönhofer, & Isaia, 2019) |
| **Absolute depth to bedrock [m]** | **Bed** | Hengl et al., 2017 | Reflects the presence of shallow subterranean habitats, especially the MSS (see discussion). |
| **Coarse fragments volumetric [%]** | **Frag** | Hengl et al., 2017 | |
| **Soil organic carbon content [g/kg]** | **Carb** | Hengl et al., 2017 | Proxy for the primary production of the area and the amount of energy reaching the subterranean habitat (Gers, 1998). |
| **Karst fissure – permeability good [binary]** | **Karst pg** | http://diktas.iwlearn.org/ | Proxy for availability of karst rock with high permeability. Proxy for areas enhancing greater dispersal potential. |
| **Karst fissure – permeability moderate [binary]** | **Karst mg** | http://diktas.iwlearn.org/ | Proxy for availability of karst rock with intermediate permeability. Proxy for areas enhancing intermediate dispersal potential. |
| Intergranular [binary] | Interg | http://diktas.iwlearn.org/ | Proxy for availability of karst rock with low permeability. |
| Impermeable [binary] | Imperm | http://diktas.iwlearn.org/ | Geological substrate that may represent non-porous areas acting as barriers to subterranean dispersal. |

we specified MaxEnt's feature classes and regularization multiplier parameters manually (Morales et al., 2017), by estimating their best configuration with the *ENMevaluate* function in the 'ENMeval' R package (Muscarella et al., 2014).

To validate models, we ran 50 bootstrap replicates of each model, keeping a random partition of 20% of the points from each run to assess predictive performance. We expressed predictive ability as the Boyce index (Boyce et al., 2002), which we calculated with the *ecospat.boyce* function in the 'ecospat' R package (Broennimann et al., 2018). This is an appropriate metric for presence-only models (Hirzel et al., 2006). Once each model had been validated, we generated a final model using the entire set of occurrence points and projected it within the accessible area. We estimated the relative contribution of each variable to the construction of the final models via permutation importance.

### 2.4 | Niche partitioning

We represented the species' ecological niche spaces as *n*-dimensional hypervolumes (Hutchinson, 1957), which we constructed with the 'hypervolume' R package (Blonder, 2018b). We generated hypervolumes using the non-collinear continuous variables introduced in the SDMs. We rescaled each variable by subtracting mean and dividing by standard deviation (pooling the data for all species), to achieve the same dimensionality for all hypervolumes' axes (Blonder et al., 2014, 2018). We delineated hypervolume with a Gaussian kernel density estimator (Blonder et al., 2018), and estimated the optimal bandwidth for each axis through cross-validation (Duong & Hazelton, 2005).

We characterized each niche by calculating total hypervolume's volume, dispersion and evenness (Mammola & Cardoso, 2020) using the 'BAT' R package (Cardoso et al., 2015, 2020). We assessed pairwise niche

differentiation among hypervolumes of the four species using both a measure of similarity (β diversity) and of distance (distance between centroids). While the measure of similarity is designed to explore the net overlap among hypervolumes, the distance between centroids provides empirical information about hypervolumes' spatial position relatively to one another, namely, how far they are in the multidimensional space (Mammola, 2019b). We estimated β-diversity through the *kernel.beta* function (Mammola & Cardoso, 2020), decomposing overall differentiation ($\beta_{total}$) into two components: the replacement of space between hypervolumes ($\beta_{replacement}$), and net differences between the amount of space enclosed by each hypervolume ($\beta_{richness}$). $\beta_{replacement}$ is meant to reflect niche shift processes and $\beta_{richness}$ variations in niche volume of one species with respect to the other (i.e. expansion or contraction) (Carvalho & Cardoso, 2020). $\beta_{total}$ ranges continuously between 0 (identical niches) and 1 (fully dissimilar niches), and $\beta_{total} = \beta_{replacement} + \beta_{richness}$.

### 2.5 | Morphological traits related to trophic specialization

We assessed morphological differentiation among species by using traits related to feeding specialization, which in Dysderidae are expressed as the ratios of basal cheliceral segment and cheliceral fang length to the carapace length (Rezač et al., 2008). Specifically, Rezač et al. (2008) divided the *Dysdera* chelicerae into five categories based on their morphology, demonstrating that species with elongated chelicerae [basal cheliceral segment length/carapace length (BS/C) ≥0.47; fang length/carapace length (F/C) ≥0.45] or with modified fang were specialists for feeding on woodlice, while the ones with unmodified cheliceral morphology (BS/C ≤ 0.34 and F/C ≤ 0.41) were generalists.

We measured those ratios in ten adult individuals per each of the four studied species (five males and five females), except for *S. hadzii* for which only four adult males were available (Appendix S1). We tested for differences in the ratio among species and sexes with analysis of variance (ANOVA).

## 3 | RESULTS

### 3.1 | Phylogenetic relationships among species

Results of the phylogenetic analyses are shown in Figure 3. Both methods recovered the same tree topology: all Rhodinae genera were confirmed as monophyletic, and three *Stalita* species were recovered as congeneric, *S. hadzii* and *S. tenaria* being more

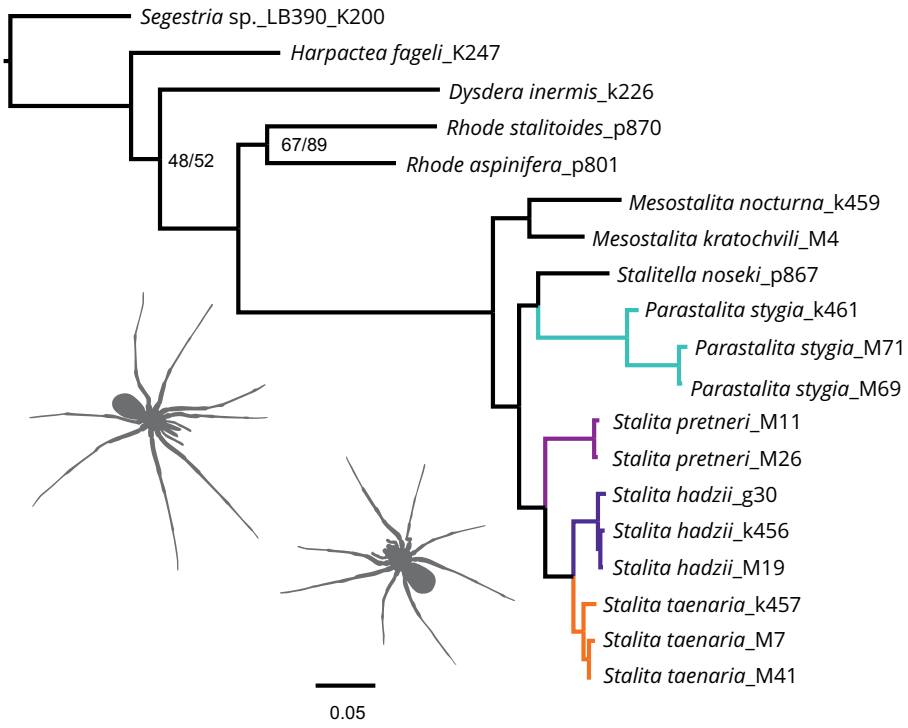


**Figure 3** | Maximum likelihood tree inferred from a concatenated matrix of five markers. Numbers next to nodes correspond to maximum likelihood bootstrap values on the left, and Bayesian posterior probabilities on the right. Nodes without support values are supported with both methods: >75 bootstrap support and >95 Bayesian posterior probabilities. The tree was rooted with *Segestria* sp., a member of Segestridae, a sister family to Dysderidae

closely related, and sister to *S. pretneri*. *Parastalita* was recovered as sister to *Stalitella*, the genus occurring in the south of the Dinarides (Deeleman-Reinhold, 1971), and the two of them as sister to *Stalita*.

### 3.2 | Species distribution modelling

As a result of collinearity analysis (Appendix S2), we selected the following variables for modelling each species' distribution: average temperature, precipitation, absolute depth to bedrock, coarse fragments volumetric, soil organic carbon content and karst fissure-permeability good and moderate. The number of occurrences used to model the distribution of each species is given in Table 2. The estimated optimal MaxEnt configuration was linear feature class for all species and, additionally, quadratic feature classes for *P. stygia* and *S. taenaria*; the optimal regularization parameter was 0.5 for *P. stygia* and *S. pretneri* and 1.5 for *S. hadzii* and *S. taenaria*.

All models had a good explanatory ability (all Boyce indexes >0.6; average of 50 bootstraps; Table 2). The model for *P. stygia* predicted a slightly wider suitable area in the northern part of the species distribution, in regions where *S. hadzii* and *S. taenaria* occur (Figure 4a). Conversely, the model failed to predict suitable areas in the southernmost edge of *P. stygia* distribution. The model for *S. pretneri* predicted a core distribution area in the central part of the northern Dinaric karst, as well as some suitable areas north-west to the known localities, which overlap with the regions inhabited by *S. hadzii* and *S. taenaria* (Figure 4b). The projected distribution for *S. hadzii* slightly overextended westward and southward, corresponding to karstic areas occupied by one of the other three species (Figure 4c). And finally, for *S. taenaria*, the model predicted a wider suitable area in the south and east directions, although with low probability (Figure 4d). *Stalita hadzii* and *S. pretneri* are found in the east and south-east areas, respectively, while in the south direction, in the area of north Adriatic islands, no cave-dwelling Dysderidae have been recorded so far. The model failed to predict suitable areas, or predicted low probability, in the south-west part of the species distribution. In general, for all species there are regions inside their current distributions with a high probability of suitable habitats, but with no records, indicating possible under-sampled areas.

Climatic variables were the most important predictors of species distributions. For *P. stygia*, precipitation alone explained more than 70% of the modelled distribution, and together with temperature more than 80% (Table 2). Similarly, for *S. taenaria*, climatic variables explained 73% of the modelled distribution. The presence of highly permeable rocks was important for *S. taenaria* (20%) and *S. hadzii* (33%), whereas other karst layers turned out to be unimportant drivers of the distribution of all species. Fragmentation explained almost 30% of the modelled distribution for *S. hadzii* and *S. pretneri*, while the effect of other soil variables was negligible in all models. *Stalita hadzii* was the only species for which karst and soil features were more important than climatic variables, cumulatively explaining more than 60% of the modelled distribution.

### 3.3 | Niche overlap

As emphasized by the generally short distance between niche centroids, species niches were close to each other in the multidimensional space (Figure 5).

**Table 2** | Statistics about the species distribution models and hypervolume analyses. Variables abbreviations are given in Table 1

| | | | Permutation Importance | | | | | | | Hypervolume | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Number | Boyce (mean±SD) | Prec | Temp | Frag | Carb | Bed | Karst mp | Karst pg | Volume | Dispersion | Evenness |
| *Parastalita stygia* | 129 (118) | 0.83 ± 0.09 | 71.3 | 10.6 | 11.0 | 1.7 | 1.9 | 2.8 | 0.7 | 1727.5 | 4.2 | 0.05 |
| *Stalita taenaria* | 99 (91) | 0.82 ± 0.08 | 46.0 | 27.0 | 4.2 | 1.7 | 0.5 | 0.0 | 20.0 | 2415.1 | 4.4 | 0.05 |
| *Stalita pretneri* | 30 (28) | 0.79 ± 0.13 | 49.2 | 7.3 | 29.4 | 10.3 | 3.9 | 0.0 | 0.0 | 1189.6 | 4.0 | 0.05 |
| *Stalita hadzii* | 24 (24) | 0.67 ± 0.26 | 28.5 | 10.4 | 26.3 | 0 | 2.2 | 0 | 32.6 | 93.4 | 2.7 | 0.04 |

***Note:***
Number = Number of occurrence records (in parentheses, the number of records after correcting for spatial sampling heterogeneity).
Boyce = Boyce index (mean ± SD of 50 runs).

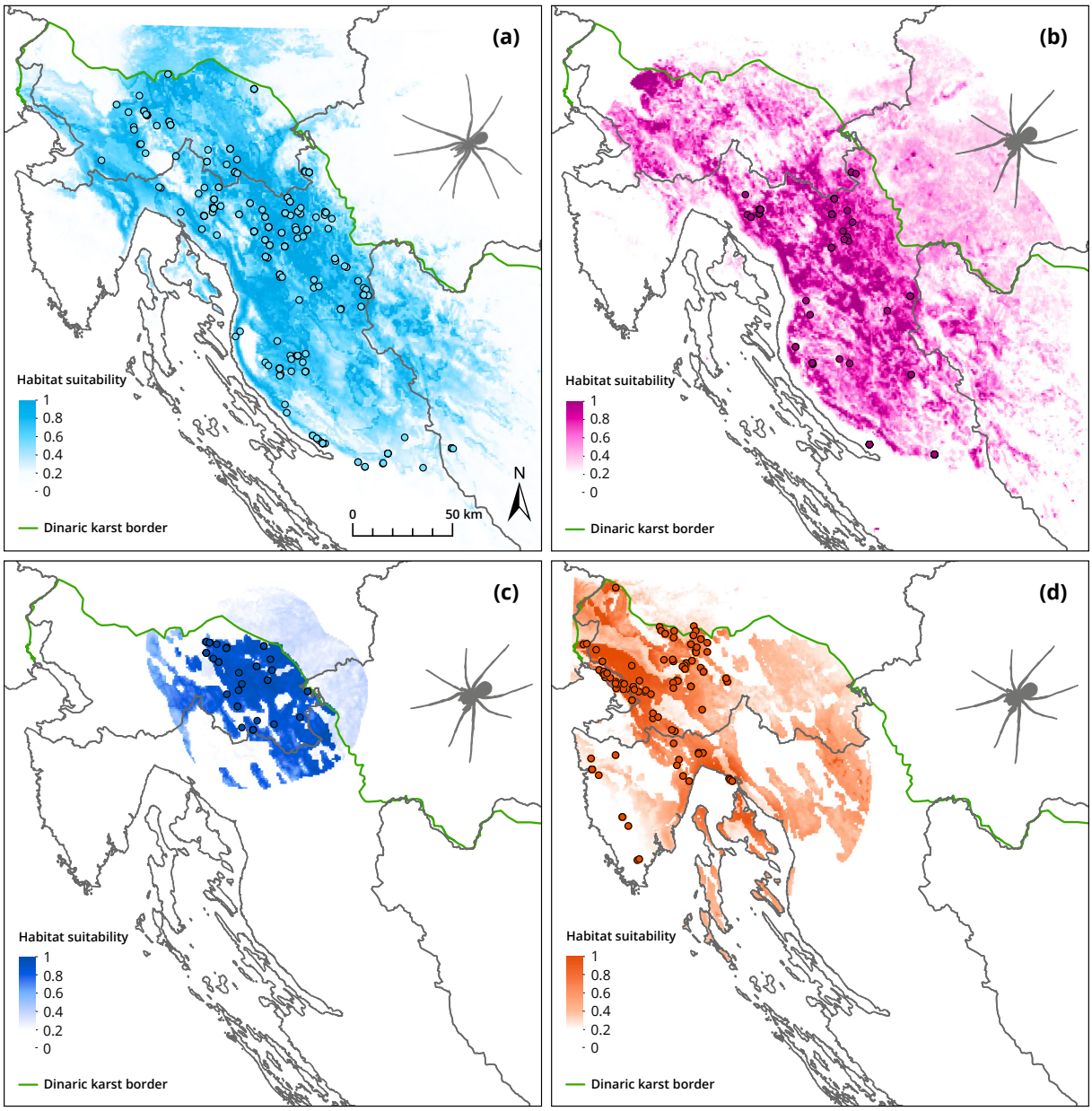


**Figure 4** | Potential distributions of the four studied species as projected by species distribution models. Circles represent occurrences. **(a)** *Parastalita stygia*, **(b)** *Stalita pretneri*, **(c)** *S. hadzii* and **(d)** *S. taenaria*

Pairwise β-diversity values pointed to the existence of both niche contraction and shift processes (Table 3). *Stalita hadzii* had the narrowest niche (volume of hypervolume two orders of magnitude less voluminous than that of the other species; Table 2), which was mostly nested within niches of the other three species, indicating niche contraction. This is also shown by the narrow range of actual environmental conditions experienced by *S. hadzii* (Figure 6). *Stalita taenaria* had the broadest and most dispersed niche (Table 2), quite dissimilar to all the other species ($\beta_{total}$ values all above 0.6; Table 3). The high values of pairwise $\beta_{replacement}$ with respect to *P. stygia* and *S. pretneri* (Table 3) also indicate a niche shift in the direction of exploiting more humid and warmer regions, whereas differences with *S. hadzii* were only attributable to $\beta_{richness}$ (Figure 5). Also, *S. taenaria* in general tolerates a wider range of temperature and humidity (precipitation) conditions (Figure 6).

*Parastalita stygia* and *S. pretneri* had the most similar niches, which is not surprising considering that the

distribution area of the two species overlaps to a great deal; in fact, they coexist in 18 caves. Niches of *P. stygia* and *S. taenaria* were only moderately similar (Table 3), reflecting their coexistence in only 9 caves and only in a part of *S. taenaria* distribution area. The greater niche dissimilarity between *P. stygia* and *S. hadzii* (Table 3) was also reflected in the fact that they were never found in the same cave, although *P. stygia*'s distribution circumscribes *S. hadzii* ones.

### 3.4 | Trophic segregation

Measured morphological traits evidenced a significant differentiation between *Parastalita* and *Stalita* (Figure 7), supporting their trophic segregation. Following the work by Rezač et al. (2008), we can infer that *Stalita* species are generalists as they have unmodified chelicerae, while *P. stygia*, with its elongated chelicerae ('slightly elongated' category sensu; Rezač et al. (2008)) is a specialist.

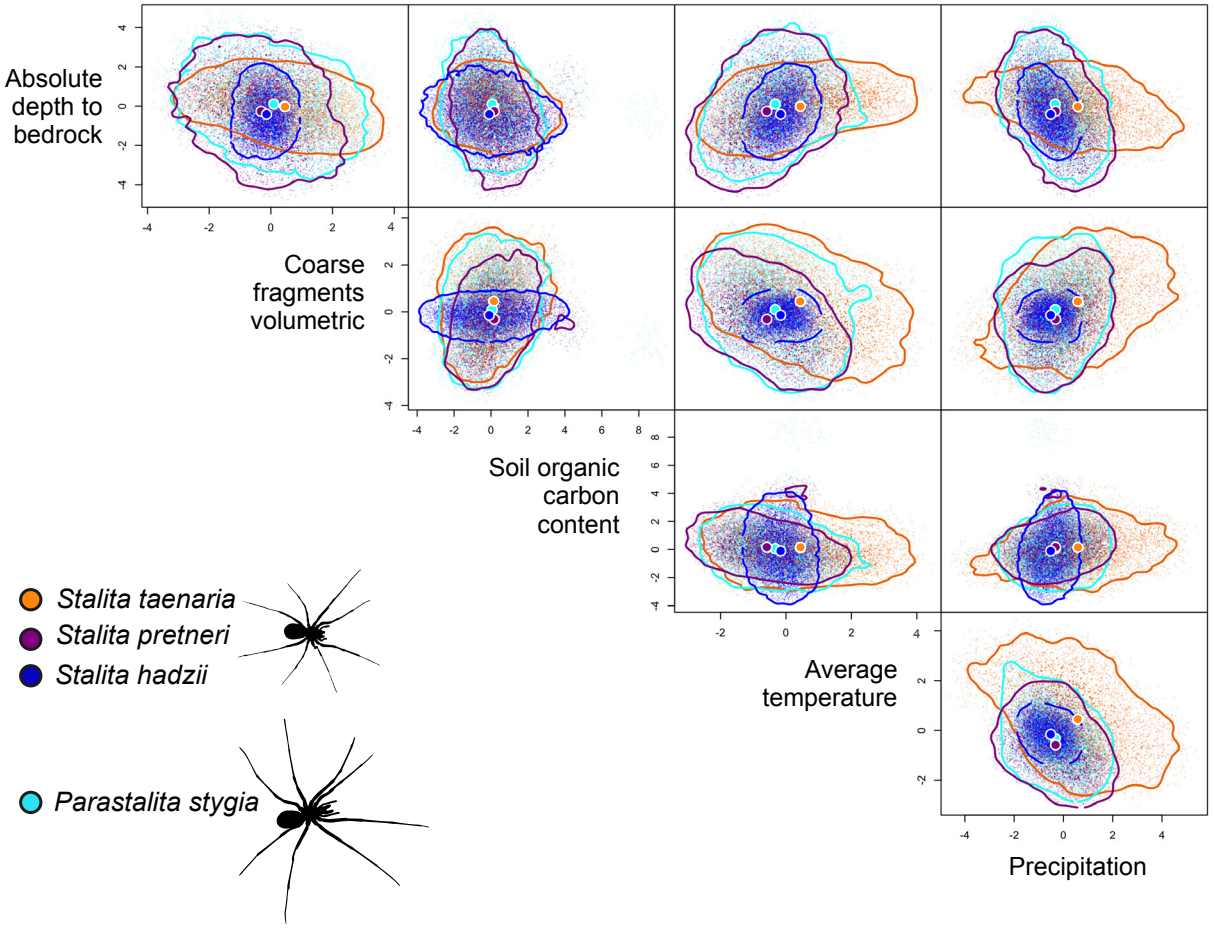


**Figure 5** | Pair plots showing the estimated five-dimensional hypervolumes for *Parastalita stygia, Stalita hadzii, S. pretneri* and *S. taenaria*. The cloud of coloured points for each species is composed of 5,000 points stochastically sampled from the inferred hypervolume, and represents the real hypervolume boundary. Contour lines are drawn for visual presentation. Variables are rescaled. Metrics relative to each hypervolume are in Table 2, whereas pairwise β-diversity and distance between centroid in Table 3

| | *Parastalita stygia* | *Stalita hadzii* | *Stalita pretneri* | *Stalita taenaria* |
|---|---|---|---|---|
| ***P. stygia*** | - | 0.61 | 0.59 | 1.25 |
| ***S. hadzii*** | 0.95 = 0.01 + 0.94 | - | 0.59 | 1.45 |
| ***S. pretneri*** | 0.39 = 0.09 + 0.30 | 0.93 = 0.02 + 0.91 | - | 1.68 |
| ***S. taenaria*** | 0.65 = 0.42 + 0.23 | 0.97 = 0.01 + 0.96 | 0.76 = 0.34 + 0.42 | - |

**Table 3** | Pairwise niche differentiation among n-dimensional hypervolumes of the four species, as estimated through a measure of overlap (below the diagonal; $\beta_{total} = \beta_{replacement} + \beta_{richness}$) and of distance (above the diagonal; distance between centroids)

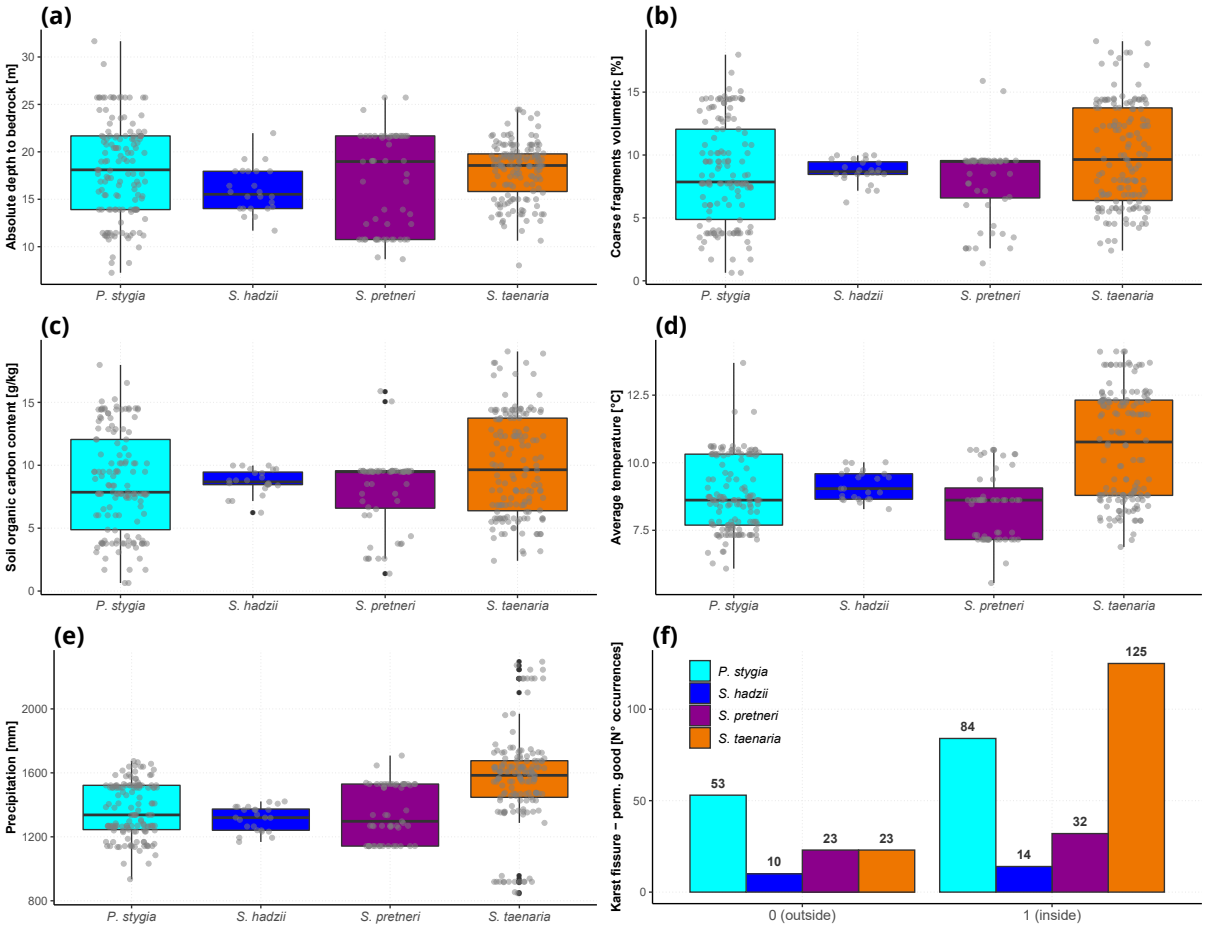


**Figure 6** | Environmental conditions experienced by the four species across their distribution range. Grey dots in a–e represent the real extracted values, whereas black dots represent outliers

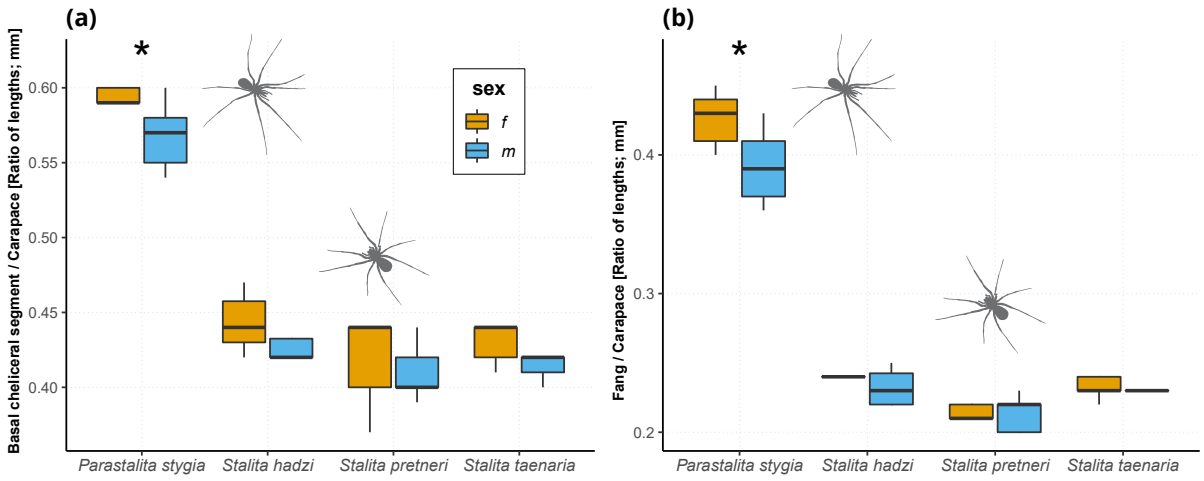


**Figure 7** | Differentiation in the chelicerae and fang shape among the four species. (a) Ratio between the length of the basal cheliceral segment and the carapace. There was a significant difference in the ratio of Parastalita stygia versus all Stalita species based on ANOVA ($F_{3,35} = 107.6$, $p < 0.001$; asterisk), as well as between males and females of each species ($F_{1,35} = 5.8$, $p = 0.030$). A post hoc Tukey test showed that all Stalita species were not significantly different from each other at $p < 0.05$. (b) Ratio between the length of the fang and the carapace. There was a significant difference in the ratio of P. stygia versus all Stalita species based on ANOVA ($F_{3,35} = 317.3$, $p < 0.001$; asterisk), whereas the differences between sexes only approached statistical significance ($F_{1,35} = 3.8$, $p = 0.058$). A post hoc Tukey test showed that all Stalita species were not significantly different from each other at $p < 0.05$

# 4 | DISCUSSION

## 4.1 | Niche differentiation in closely related species

We showed that multiple niche-based processes are responsible for the current distribution patterns of our model species at the restricted spatial scale of the northern Dinaric karst. Three congeneric species, *S. taenaria*, *S. hadzii* and *S. pretneri*, do not overlap in their distributions. Competition could be an important factor determining their distribution patterns, given that *Stalita* species are almost identical in all somatic characters (Deeleman-Reinhold, 1971; Kratochvíl, 1970) as well as in the cheliceral morphology (Figure 7). On the other hand, the distribution of the fourth species, *P. stygia*, largely overlays with that of *S. pretneri*, and to a smaller extent, with that of *S. taenaria*. In at least 27 of 255 caves included in the distribution database, *P. stygia* has been found coexisting with other *Stalita* species.

We found that niche differentiation is not strictly related to phylogenetic history: closely related species from a genetic standpoint (*S. taenaria* and *S. hadzii*) are not the most similar in terms of ecological niche. At the same time, *S. pretneri* has a more similar niche to the distantly related *P. stygia* than to its congenerics. This would suggest that the ecological specialization in this complex of species is evolving in response to recent adaptive pressures. This finding parallels the phenomena observed in crustacean inhabiting groundwaters (Trontelj et al., 2012), but also in other subterranean spiders, such as *Troglohyphantes* species in the Western Alps (Mammola, et al., 2020). *Stalita pretneri* has the largest distribution among the three *Stalita* species, stretching over 160 km (Figure 2) and overlapping to a great extent with the distribution of *P. stygia*. In the majority of caves where *S. pretneri* lives in, the two species co-occur. This should translate to a direct competition, since the two species are of comparable size and occupy similar microhabitats. A possible mechanism explaining their coexistence could be a shift in the trophic niche of *P. stygia* towards a more specialized diet. In several *Dysdera* species, elongation of chelicerae (Arnedo et al., 2007; Rezač et al., 2008) and shift in nutritional physiology (Toft & Macías-Hernández, 2017; Vizueta et al., 2019) have been shown to be critical adaptations for feeding on woodlice (Crustacea: Isopoda). Woodlice have evolved an array of morphological, chemical and behavioural defensive mechanisms that make them repulsive and unapproachable for many predatory arthropods (Gorvett, 1956). They are a dominant component of the ground-dwelling fauna in caves (Deharveng & Bedos, 2019), and Dinaric caves are home to a great diversity of species, e.g. in the genus *Alpioniscus* (Bedek et al., 2019).

Our morphological analysis supports trophic segregation between *Parastalita* and *Stalita* (Figure 7). The differences between unmodified and elongated cheliceral morphology appears even more conspicuous in our case than those reported by Rezač et al. (2008) for *Dysdera*. These authors measured a fang to carapace length ratio (F/C) of 0.41 for unmodified chelicerae, 0.45 for slightly elongated and 0.55 for very elongated; in *Stalita* species we found average F/C values between 0.21 and 0.24, while it was two times higher in *P. stygia* (0.41). T he difference in the ratio of basal cheliceral segment to carapace length (BS/C) was also clear-cut, 0.42–0.44 for *Stalita* species versus 0.58 for *P. stygia* (for *Dysdera* that value is 0.34 for unmodified, 0.47 for slightly elongated and 0.72 for very elongated). So, due to its elongated chelicerae, *P. stygia* should be able to use woodlice as a food source much more effectively than *Stalita* (Figure 1c). A specialization for feeding upon an abundant prey item in Dinaric caves, which other predators cannot exploit, would give *P. stygia* an evolutionary advantage. This adaptation, coupled with the high dispersal potential through the network of fissures in this well-connected karst landscape (Barr, 1967; Culver et al., 2004), would explain the unusually broad distribution of *P. stygia* (240 km long, Figure 2) and the fact that, unlike *Stalita*, *Parastalita* individuals are often locally abundant (M. Pavlek, pers. obs.). At the same time, the difference in cheliceral morphology allows *P. stygia* to coexist with other *Stalita* species.

Niche shift seems to allow *S. taenaria* to exploit different, warmer and more humid habitats, and indeed this is the only species whose distribution stretches from the coastal areas to mountain regions (from 40 to 1,100 m a.s.l.). *Stalita hadzii* has the narrowest distribution centred in the north-east part of the Dinarides. According to $\beta_{richness}$ values, the reason for this small distribution could be niche contraction, possibly driven by the absence of karst to the north and competitive exclusion by *S. taenaria* and *S. pretneri*, distributed eastward and southward respectively.

## 4.2 | Ecological drivers of species distributions

Climatic factors, especially precipitation, are the most important predictors that explain the distributions of the studied species. Precipitation shapes general underground climatic conditions (Badino, 2010) by ensuring constantly high levels of relative humidity

(Bregović & Zagmajster, 2016). Furthermore, high precipitation regimes are associated with the input of energy (Culver et al., 2006; Mammola & Leroy, 2018), typically in the form of organic matter transferred underground by percolating waters. It is easy to infer that a higher energy input should translate into a higher abundance and diversity of animals, which in turn determines favourable conditions for apical predators such as *Stalita* and *Parastalita*.

Contrary to what was found in other studies (Christman & Culver, 2001; Pipan & Culver, 2017), karstic features are not a limiting factor of the species distribution. In this area, karst substrates are widespread and highly porous, ensuring excellent connectivity among subterranean habitats (Barr, 1967; Culver et al., 2004). Interestingly, similar broad north Dinaric distribution patterns have been documented for other specialized subterranean terrestrial invertebrates, such as the beetle *Leptodirus hochenwartii* Schmidt (1832) (Coleoptera: Leiodidae; Jalžić & Pretner, 1977; Pretner, 1973), and the millipede *Haasia stenopodium* Strasser (1966) (Diplopoda: Anthogonidae; Antić et al., 2015).

The presence of fragmented rocks was a further important driver of the species' distributions, particularly, *S. pretneri* and *S. hadzii*. On average, all species are found in areas where the volume of coarse rock fragments in soils is >7% (Figure 6b), and the depth of the bedrock is >10 m (Figure 6a). We introduced these variables in the models to try capturing the availability of MSS-like habitats. The so-called MSS (Mammola, et al., 2016) is a superficial subterranean habitat that originates from the accumulation of rock fragments produced by mechanical weathering of different rocky substrates. The presence of interspersed voids between rocky fragments and a soil layer insulating the system from external weather may lead to the development of a suitable habitat for the subterranean fauna. Although published data about MSS-dwelling species in the Balkan region are scarce, indirect evidence suggests that this could be an important habitat for our model species. In fact, being active hunters rather than web-builders, Dysderidae are frequently associated with MSS habitats (Mammola, et al., 2018), and different species have been collected in MSS in other areas [e.g. *Dysdera* (Arnedo et al., 2007; Pipan et al., 2010), *Harpactocrates* and *Harpactea* (Ledesma et al., 2019)]. This was, however, the first attempt to capture MSS conditions with species distribution models. The development of more specific rasters representing MSS is certainly needed to improve model performance in this sense (Mammola & Leroy, 2018).

When comparing known occurrence records with the predicted distributions for each species (Figure 4), we observed important distribution gaps. This could be due to the model overestimating species distributions or due to under-sampling, a well-known problem in subterranean biology. Research efforts in exploring subterranean habitats are often concentrated in certain areas, typically in more accessible caves (Zagmajster et al., 2010), whereas the vaster proportion of the subterranean domain remains unexplored (Ficetola et al., 2019; Mammola, et al., 2019). This issue is of particular relevance when it comes to modelling the distribution of subterranean species (Mammola & Leroy, 2018), but also to estimate species richness patterns (Zagmajster et al., 2008, 2010). For example, in the case of *S. pretneri*, one explanation for large gaps throughout its distribution could be under sampling due to its elusive nature (the species is rarely found and always in low numbers), as well as the lack of investigations in the MSS.

# 5 | CONCLUSION

This is the first study on the ecological niche of specialized subterranean Dysderidae, and of any obligatory cave-dwelling species or species group in the Dinaric karst. We demonstrated that cave-dwelling spiders can be effectively used as models to revisit classical niche theory. By showing that species' distributions are shaped by both abiotic conditions and competition, we emphasized how even simplified environments still maintain the potential for diversification *via* niche differentiation. We demonstrated that: (a) phylogenetic relatedness does not reflect niche similarity; (b) closely related species have adapted to different climatic conditions, thereby attaining disjunct distributions, and (c) the prerequisite for sympatry between *Parastalita* and *Stalita* is morphological (dietary) segregation. With the accumulation of further knowledge, it will be possible to revisit these processes to account for the interactions with other members of the subterranean community, thereby providing niche-based explanations for the origin and evolution of subterranean biological diversity of the Dinaric karst.

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## DATA AVAILABILITY STATEMENT

DNA sequences are deposited in GenBank® (see accession codes in Appendix S1). Occurrence points used in this study are available in figshare (https:// doi.org/10.6084/m9.figsh are.12613193). Coordinates for part of the caves were taken from 'GeoRef' portal (http://www.georef.hr/) and 'Bioportal – Katastar speleoloških objekata RH' (http://www.biopo rtal.hr/ gis/), hosted by Institute for Environment and Nature of Croatia. All environmental variables used in the models are available from public repositories (Diktas project website, http://diktas.iwlea rn.org/; SoilGrids database, Hengl et al., 2017; and WorldClim website, Fick & Hijmans, 2017).

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